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DIETS OF NORTHERN BARRED OWLS AND NORTHERN SPOTTED OWLS IN AN AREA OF SYMPATRY

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ABSTRACT.—We compared diets of Northern Barred Owls (*Strix varia varia*) and Northern Spotted Owls (*Strix occidentalis caurina*) in western Washington during 1985–89. Diets of both species were dominated by nocturnal mammals, but diets of Barred Owls included a more diverse and more even distribution of prey. Estimated dietary overlap between the two species based on the Pianka Index was 76%. Barred Owl diets included more terrestrial mammals, more birds, more diurnal prey, and more prey that were associated with riparian areas, including fish, amphibians, and snails. The snowshoe hare (*Lepus americanus*) comprised 35% of prey biomass in the diet of Barred Owls. The diet of Spotted Owls was dominated by the northern flying squirrel (*Glaucomys sabrinus*), which comprised 51% of prey numbers and 57% of prey biomass. We speculate that Barred Owls and Spotted Owls compete for food because their diets overlap considerably, their food appears to be limiting in many years, and Barred Owls are gradually invading territories historically occupied by Spotted Owls.

KEY WORDS: *Northern Barred Owl*; Strix varia varia; *Northern Spotted Owl*; Strix occidentalis caurina; *diet*; *competition*; *predation*; *Washington.*

Dietas de *Strix varia varia* y *Strix occidentalis caurina* en un area simpatrica.

RESÚMEN.—Comparamos las dietas de *Strix varia varia y Strix occidentalis caurina* en el oeste de Washington durante 1985–89. En las dietas de ambas especies predominaron los mamíferos nocturnos sin embargo la dieta de *Strix varia* fue mas diversa y con una distribución mas uniforme de presas. Estimamos el traslape de las dietas entre las dos especies con base en el Indice de Pianka (76%). La dieta de *Strix varia* incluyó mas mamíferos terrestres, mas aves, mas presas diurnas y mas presas asociados con áreas ribereñas incluyendo peces, anfibios y caracoles. *Lepus americanus* constituyó el 35% de la biomasa de presas de la dieta de *Strix varia.* En la dieta *Strix occidentalis* predominó *Glaucomys sabrinus* con un 51% del número de presas y un 57% de la biomasa de presas. Especulamos que *Strix varia* y *Strix occidentalis* compiten por comida debido a que sus dietas se traslapan considerablemente, su alimento parece limitarse por años y debido a que *Strix varia* gradualmente esta invadiendo los territorios historicamente ocupados por *Strix occidentalis.*
[Traducción de César Márquez]

During the last century, the Northern Barred Owl (*Strix varia varia*) has gradually expanded its range westward across Canada and south into the Pacific Northwest and northern California (Grant 1966, Campbell 1973, Shea 1974, Taylor and Forsman 1976, Boxall and Stepney 1982, American Ornithologists' Union 1983, Dunbar et al. 1991, Hamer 1988, Hamer et al. 1994, Dark et al. 1998, Wright and Hayward 1998). As a result, the range of the Northern Barred Owl now almost completely overlaps the range of the Northern Spotted Owl (*Strix occidentalis caurina*) (Dark et al. 1998, del Hoyo et al. 1999). In some areas in British Columbia and

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Washington state, Barred Owls are now so abundant they outnumber Spotted Owls (Hamer 1988, Dunbar et al. 1991).

Although Barred Owls are generally believed to compete with Spotted Owls for space (Dunbar et al. 1991, Leskiw and Gutiérrez 1998), the extent to which they also compete for food is unknown. Diets of Northern Spotted Owls have been described in many areas (Barrows 1980, Forsman et al. 1984, Richards 1989, Ward 1990), but no data have been published on diets of Northern Barred Owls in the area of range overlap with the Northern Spotted Owl. During radio-telemetry studies of Barred Owls and Spotted Owls in Washington in 1985–89, regurgitated pellets were collected in roosts and nest areas to determine composition of the diets of the owls. We analyzed the pellet samples, and herein describe and compare the diets of these two closely related species in an area of sympatry.

STUDY AREA AND METHODS

We collected pellets from 12 Barred Owl territories and 28 Spotted Owl territories in western Washington. All data from Barred Owls came from the 317 km^2 study area surrounding Baker Lake on the west slope of the Cascade Range in northern Washington (Fig. 1). Most data from Spotted Owls (87% of prey items) came from 14 territories in the Baker Lake study area and nine territories in adjacent areas within the Mt. Baker-Snoqualmie National Forest (Fig. 1). Small numbers of prey from Spotted Owls were also included from four territories on the Gifford Pinchot National Forest in the southern Washington Cascades (N = 14), and one territory on the Olympic Peninsula (N = 9). Barred Owls and Spotted Owls are sympatric throughout this entire region.

The Baker Lake study area was characterized by steep-sided valleys with elevations ranging from 244 m on the valley floor to 1800 m at the upper limits of the forested zone on the slopes of Mount Baker. Mean annual precipitation was 254 cm, most of which was rain during winter (Franklin and Dyrness 1973). The study area was largely forested, except for small areas of talus, meadow, marsh, and recent clearcuts. The dominant vegetation was forests of western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*) at lower elevations, and forests of mountain hemlock (*T. mertensiana*) and Pacific silver fir (*Abies amabilis*) at higher elevations (Franklin and Dyrness 1973). Forest age varied from young stands on recent clearcuts to forests >200 yr old.

Diets were estimated primarily from prey remains in regurgitated pellets, but the sample also included a few freshly-killed prey remains found in roosts or nests. Pellets from Barred Owls were collected in 1985–89 and pellets from Spotted Owls were collected in 1986–89. Most pellets were collected during the spring and summer (April–August), and were of recent origin as indicated by the fact that they had not been washed apart by rain or snow. Thus, our analysis primarily reflects the diet during spring and summer. Some of the owls that we studied were breeding, but the breeding status of many of the owls was not known in each year.

We estimated the number of prey in pellets by counting skulls, jaws, or bones of the appendicular skeleton, whichever gave the highest count. Numbers of insects were estimated from fragments of exoskeletons. Biomass was estimated by multiplying the estimated number of individuals of each species by the estimated mean mass of each species, or by individually estimating the mass of each prey based on comparisons of skeletal remains with specimens of known age and mass. Estimates of mean mass were obtained from a variety of sources, including Maser et al. (1981), Chapman and Feldhamer (1982), Steenhof (1983), and Forsman et al. (1984). All comparisons were based on the combined sample for all owls, because samples were too small to estimate average diets for individual territories.

We used the modified Simpson's Index (Odum 1975, Simpson 1949) to estimate dietary diversity, and the modified Hill Ratio (Hill 1973, Alatalo 1981) to estimate evenness of prey in the diet. These indices range from 0–1, with larger values indicating greater diversity or evenness. If all prey were taken in equal numbers, then dietary evenness would be 1. We used Pianka's Index (Pianka 1973) to compare dietary overlap; this index yields values from 0–1 (no overlap to complete overlap, respectively). All estimates of dietary diversity, evenness and overlap were based on prey numbers.

To evaluate differences in timing of foraging and habitats used for foraging, we grouped prey based on their primary period of activity (nocturnal, diurnal, both), primary habitat association (forest, riparian, meadow, talus), and primary behavior type (arboreal, semiarboreal, terrestrial/aquatic). We then used χ^2 tests to compare the relative propor-

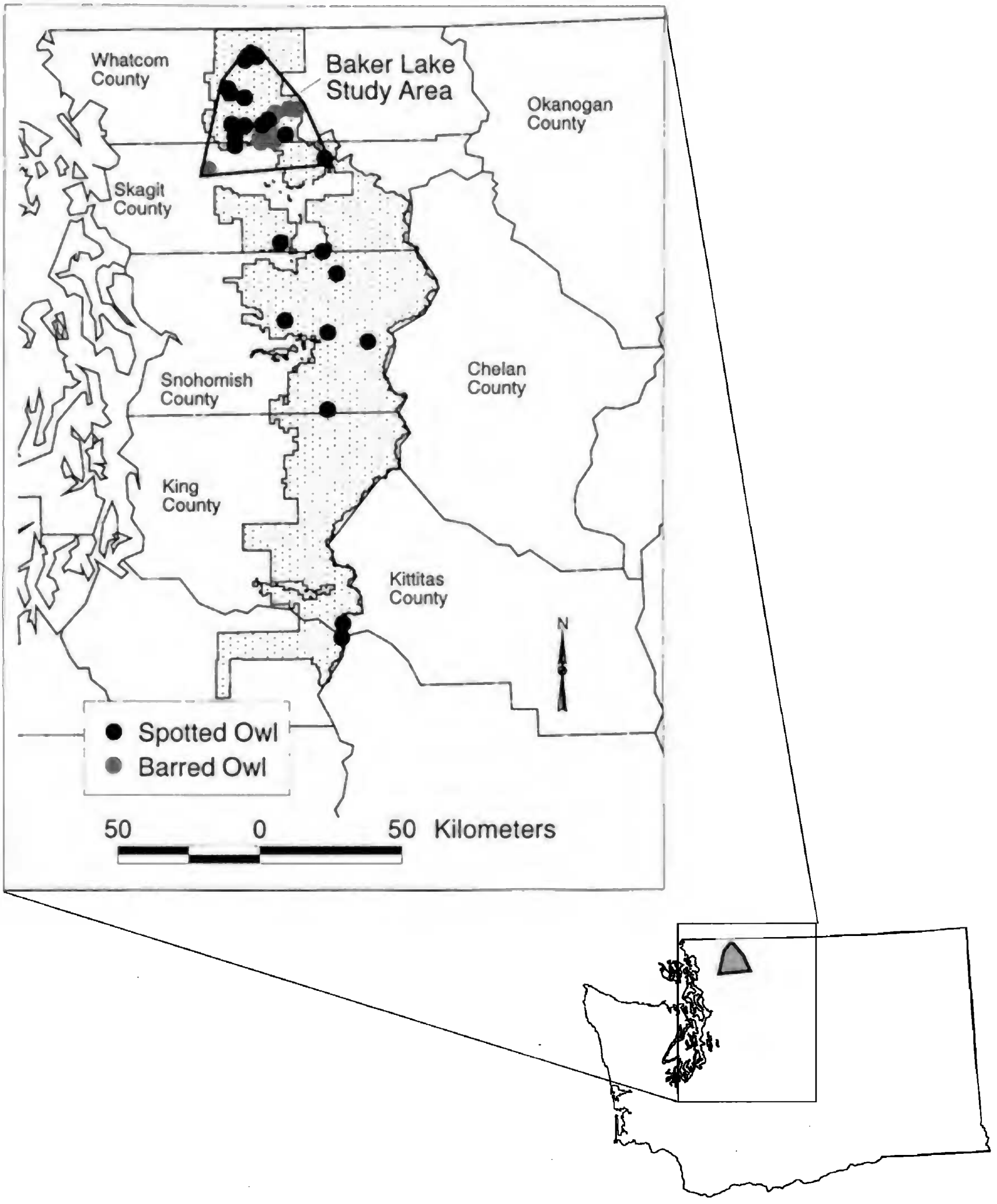

Figure 1. Locations where pellets were collected from Northern Barred Owls and Northern Spotted Owls on the Mt. Baker-Snoqualmie National Forest (stippled area) in northwestern Washington, 1985–89.

Table 1. Percent numbers (Num) and biomass (Bio) of prey in samples of pellets collected from Northern Barred Owls and Northern Spotted Owls in western Washington, 1985–89.

	Barred Owls			Spotted Owls		
Prey	N[a]	% Num	% Bio[b]	N[a]	% Num	% Bio[b]
Mammals	202	76.1	74.5	285	96.2	98.6
Sorex spp.	26	9.8	0.4	11	3.7	0.2
Neurotrichus gibbsii	20	7.6	0.6	1	0.3	tr[c]
Scapanus spp.	17	6.4	2.9	—	—	—
Ochotona princeps	—	—	—	9	3.0	4.8
Lepus americanus	22	8.3	35.0	9	3.0	13.4
Tamias townsendii	2	0.7	0.5	—	—	—
Tamiasciurus douglasii	22	8.3	14.1	5	1.7	3.6
Glaucomys sabrinus	53	20.0	18.4	150	50.7	58.1
Thomomys talpoides	—	—	—	1	0.3	0.3
Peromyscus maniculatus	18	6.8	1.2	61	20.6	4.5
Neotoma cinerea	—	—	—	13	4.4	11.6
Clethrionomys gapperi	3	1.1	0.2	20	6.8	1.6
Microtus spp.	2	0.7	0.2	—	—	—
Microtus oregoni	16	6.0	0.9	2	0.7	0.1
Zapus trinotatus	1	0.4	0.1	1	0.3	0.1
Mustela erminea	—	—	—	2	0.7	0.3
Birds	29	11.0	19.4	8	2.8	1.4
Bonasa umbellus	6	2.3	11.3	—	—	—
Otus kennicottii	1	0.4	0.4	—	—	—
Corvus spp.	3	1.1	4.2	—	—	—
Unident. small bird	19	7.2	3.5	8	2.8	1.4
Miscellaneous	34	12.9	6.1	3	1.0	tr[c]
Fish (small salmonids)	7	2.6	4.7	—	—	—
Amphibians (frogs)	15	5.7	1.4	—	—	—
Molluscs (snails)	2	0.8	tr[c]	—	—	—
Insects	10	3.8	tr[c]	3	1.0	tr[c]
Totals	265	100.0	100.0	296	100.0	100.0

[a] Indicates number of individual prey identified in pellets.
[b] Total biomass was 32 745 g for Barred Owls and 29 154 g for Spotted Owls.
[c] tr ≤ 0.05%.

tion of prey biomass in different categories. Each species was assigned to only one activity period, habitat association, and behavior type, with the exception of snowshoe hares (*Lepus americanus*) which were split evenly between forest and riparian habitats. Although snowshoe hares were sometimes active during the day, we labeled them as nocturnal because they are most active at night (Keith 1964).

Results

We identified 265 prey items from 13 Barred Owl territories and 296 prey items from 26 Spotted Owl territories (Table 1). Diets of Barred Owls included ≥24 species, and diets of Spotted Owls included 17 species. The sample of prey from Spotted Owls was dominated by mammals, which comprised 96.2% of prey numbers, and 98.6% of prey biomass. In contrast, Barred Owl diets included only 76.1% mammals, with the balance made up of birds, fish, frogs, snails, and insects. In terms of total biomass, the most important prey in diets of Spotted Owls and Barred Owls were northern flying squirrels (*Glaucomys sabrinus*) and snowshoe hares, respectively.

Mean mass of individual prey captured by Barred Owls and Spotted Owls was 123.6 and 98.5 g, respectively. Both species captured prey in a broad range of size categories, up to and including snowshoe hares weighing about 1000 g each. However, diets of Spotted Owls were dominated by prey

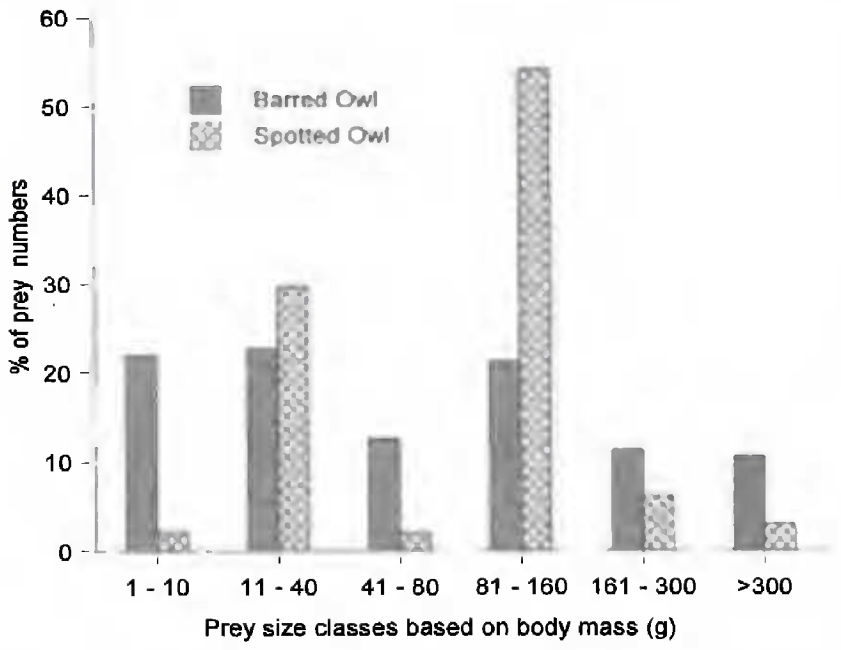

Figure 2. Distribution of prey by size class in diets of Northern Spotted Owls and Northern Barred Owls in western Washington, 1985–89.

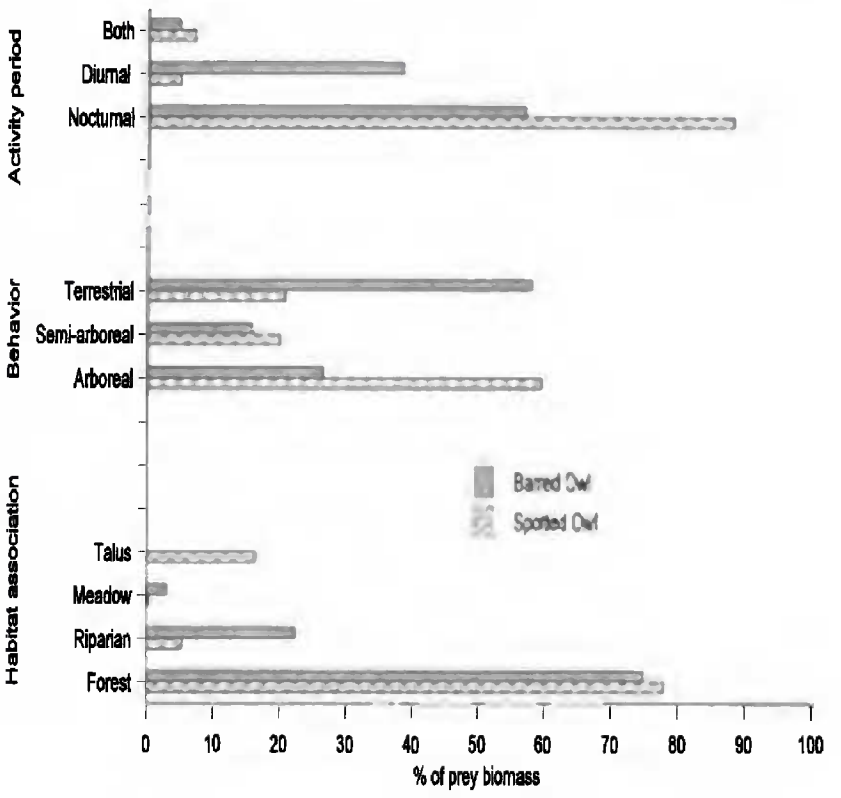

Figure 3. Diets (% of total biomass) of Northern Spotted Owls and Northern Barred Owls in western Washington, subdivided based on habitat associations, behavior types, and primary activity periods of prey.

in the 81–160 g range, whereas prey taken by Barred Owls were more evenly distributed across all prey-size categories (Fig. 2).

The diet of Barred Owls was considerably more diverse than the diet of Spotted Owls (Simpson Index = 0.917 vs. 0.699). The distribution of prey in the diet of Barred Owls was also more even than in the diet of Spotted Owls (Hill Index = 0.814 vs. 0.533). That is, Barred Owls captured many different kinds of prey in similar numbers, whereas Spotted Owls tended to concentrate on a few kinds of prey. The Pianka Index of dietary overlap between the two species was 0.76.

Diets of both species were dominated by nocturnal animals, but Barred Owl diets included more diurnal prey (Fig. 3, $\chi^2_2 = 64.7$, $P < 0.001$). Barred Owl diets were also dominated by terrestrial species, whereas Spotted Owl diets were dominated by arboreal or semiarboreal species, especially northern flying squirrels and bushy-tailed woodrats (*Neotoma cinerea*) (Fig. 3, Table 1, $\chi^2_2 = 72.4$, $P < 0.001$). Diets of both species were dominated by animals associated with forest habitats, but diets of Barred Owls included more species associated with riparian areas, swamps, or meadows, and fewer species associated with talus (Fig. 3, $\chi^2_3 = 62.3$, $P < 0.001$). Diets of Spotted Owls included 16.4% biomass from mammals associated with rock outcrops or talus, such as bushy-tailed woodrats and pikas (*Ochotona princeps*), whereas none of the prey captured by Barred Owls were typically associated with rock outcrops or talus (Fig. 3).

DISCUSSION

Our results indicated that Northern Spotted Owls preyed on a fairly broad range of prey, but primarily focused on a few species of mammals. That is, the distribution of prey in the diet was very uneven. In contrast, the Barred Owl was more of a generalist, preying on a broader range of species at lower frequencies. This finding agrees with previous studies in which diets of Northern Spotted Owls were generally dominated by a few types of arboreal or semiarboreal forest mammals (Barrows 1980, Forsman et al. 1984, 2001, Ward 1990), whereas diets of Barred Owls typically include a diverse mixture of prey (Bent 1938, Hodges 1947, Smith 1952, Sweeny 1959, Korschgen and Stuart 1972, Rhodes 1974).

Although both species hunted primarily in forests, the composition of the diet suggested that Barred Owls made greater use of meadows and riparian areas than did Spotted Owls. During the study, we often observed Barred Owls perched at the edge of marshes and ponds, or directly above small streams (unpubl. data). A sample of pellets collected from two Barred Owl territories in western Montana included mostly microtines associated with meadows and riparian areas (Marks et al. 1984).

Potential sources of variation in our data included differences among years, territories, and breed-

ing status. We did not have enough data to stratify the samples and evaluate these effects. However, Spotted Owl territories in the Baker Lake study area often overlapped two or more Barred Owl territories and the habitat composition of Barred and Spotted Owl home ranges showed few differences (unpubl. data), indicating both species of owls were likely feeding on similar prey populations. Similarly, Herter and Hicks (2000) found considerable overlap in the kinds of forests occupied by Barred Owls and Spotted Owls in the central Cascades of Washington. Therefore, we believe that the differences we observed were primarily the result of differences in prey selection as opposed to differences in prey availability.

The high proportion of diurnal animals in Barred Owl pellets suggested that these owls were more active during the day than were Spotted Owls. This was confirmed from observations of radio-marked Barred Owls on the Baker Lake study area, which moved, on average, 131 m/hr during the day and 260 m/hr at night (unpubl. data). Spotted Owls studied by Sovern et al. (1994) in the Washington Cascades only moved 20.6 m/hr on average during the day.

Although the distribution of prey species in pellets of Barred Owls was more diverse and more even than in pellets of Spotted Owls, the 76% overlap in the two samples suggested that the two species may compete for food, especially if prey becomes limiting. That prey is limiting for Spotted Owls and many other species of owls in the northern hemisphere seems likely, given that they do not breed in many years (Southern 1970, Adamcik et al. 1978, Mikkola 1983, Forsman et al. 1984, 1996, Hayward and Garton 1988).

Some previous comparisons of dietary composition in owls have shown clear differences between species, but others have demonstrated considerable overlap between some species (e.g., Korschgen and Stuart 1972, Marti 1974, Herrera and Heraldo 1976, Hayward and Garton 1988). However, high dietary overlap does not necessarily prove that species compete for food because they can still avoid direct competition by foraging in different areas or at different times. Our data suggested some species-specific differences in timing and location of foraging, but for the most part, Barred Owls and Spotted Owls were similar in that they were primarily nocturnal and foraged primarily in forests. Therefore, we suggest that the above mentioned approaches to avoiding competition were not particularly effective in this case, especially in view of the fact that Barred Owls have recently invaded and taken up residence in areas traditionally occupied by Spotted Owls.

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